Zootaxa 3320: 61–68 (2012)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Discovery and redescription of type material of *Nausithoe simplex* (Kirkpatrick, 1890), comb. nov. (Cnidaria: Scyphozoa: Coronatae: Nausithoidae) from the North Atlantic

ANDRÉ C. MORANDINI[1] & GERHARD JARMS[2]

[1]*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, n. 101, São Paulo, SP, 05508-090, Brazil*

[2]*Biozentrum Grindel und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany*
E-mails: acmorand@ib.usp.br; andre.morandini@gmail.com; Gerhard.Jarms@zoologie.uni-hamburg.de

Abstract

With discovery and examination of type specimens in the Natural History Museum, London, UK, we reassign *Stephanoscyphistoma simplex* (Kirkpatrick, 1890) to the genus *Nausithoe* Kölliker, 1853, as *Nausithoe simplex*, comb. nov., and designate a lectotype for the species. Use of morphometric measurements is considered important in coronate systematics, but key features also include the unique whorl of internal cusps and the shape of these cusps. All previous records of *N. simplex* must be re-evaluated, taking into consideration the morphology of these internal cusps.

Key words: *Stephanoscyphus*, *Nausithoe*, polyp, systematics, taxonomy, *Stephanoscyphistoma*

Introduction

The order Coronatae Vanhöffen, 1892 is considered the basal group of the class Scyphozoa Goette, 1887 based on both older (Thiel 1966; Uchida 1969; Werner 1973) and more recent studies (Marques & Collins 2004; Collins *et al*. 2006; Bayha *et al.* 2010). About 60 species are currently known in the group (Morandini & Jarms *in prep*.). Several authors (Werner 1973; Jarms 1990; Silveira & Morandini 1997) have stated that life cycle studies are essential in resolving systematics of the order, especially in metagenetic species. As a consequence, the study of metagenesis and its variations are decisive for establishing evolutionary traits among coronates (Jarms 2010).

Coronate polyps are characteristic animals having a striking feature, namely a peridermal tube surrounding their soft tissues (Werner 1970) that distinguishes them from other scyphozoan polyps (subclass Discomedusae Haeckel, 1880) (Chapman 1966). They are nevertheless often overlooked or mistaken for polychaete tubes in the sorting of benthos samples. While present in collections from many expeditions, they are seldom identified as coronate polyps even though they are amongst the most abundant taxa in certain habitats (Galil & Zibrowius 1998).

Current knowledge of the periderm tube in coronates has been reviewed in a series of papers (see mainly Jarms 1990, 1991, 1997), and summarized in a more recent one (Morandini & Jarms 2005). Based on available data it is sometimes impossible to assign specimens to family or genus (Morandini & Jarms 2005). To deal with the situation, Jarms (1990, 1991) followed provisions of the International Code of Zoological Nomenclature and introduced the collective group name *Stephanoscyphistoma* for these taxa. According to the code, collective groups are treated as genus-group names, albeit with special provisions (see "collective group", ICZN 1999: 105). Included in *Stephanoscyphistoma* Jarms, 1990 are polyps of poorly described species, or those that cannot be assigned with confidence to a medusa genus.

Morandini & Jarms (2005) retained four species of coronates in this group: *Stephanoscyphistoma allmani* (Kirkpatrick, 1890), *S. bianconis* (Thiel, 1936), *S. corniformis* (Komai, 1936), and *S. simplex* (Kirkpatrick, 1890). Due to superficial descriptions and absence of type material, it has not been possible to assign them to any known medusa genus, thereby creating instability in taxonomy of the group.

Accepted by D.R. Calder: 12 Apr. 2012; published: 22 May 2012

Of these four species, *Stephanoscyphistoma simplex* is the most inadequately described. The original account is limited to a few comments regarding structure of the tube (solitary) in comparison with that of *S. allmani* (colonial) (Kirkpatrick 1890: 14). Although Kramp (1951, 1959) provided a thorough description of *S. simplex* based on several specimens, we believe from measurement data and from current knowledge of the number and arrangement of cusps that he may have been dealing with several species.

In this communication we provide a description of *Stephanoscyphistoma simplex* (Kirkpatrick, 1890) based on discovery of Kirkpatrick´s specimens. The species can now be properly assigned within the current classification of the group.

Material and methods

Data included herein are based on examinations of preserved specimens of stephanoscyphistomae from collections at the Natural History Museum (NHM), London (UK). Measurements and scanning electron microscopy (SEM) preparations undertaken as part of the study followed procedures described by Jarms (1991) and Jarms *et al*. (2002a, b). The type series contains four solitary periderm tubes. From these, one was designated as a lectotype (NHM 1878.3.26.11a), and another one was cut and examined by SEM (NHM 1878.3.26.11d). One of the specimens (NHM 1878.3.26.11c) unfortunately comprises only the basal disc and a small piece of the tube, and has not been used for measurements.

Results

Phylum Cnidaria Verrill, 1865
Subphylum Tesserazoa Salvini-Plawen, 1978 (Medusozoa Petersen, 1979)
Class Scyphozoa Goette, 1887
Subclass Coronamedusae Calder, 2009
Order Coronatae Vanhöffen, 1892
Family Nausithoidae Haeckel, 1880
Genus *Nausithoe* Kölliker, 1853

***Nausithoe simplex* (Kirkpatrick, 1890), comb. nov.**
(Figs 1–4)

Stephanoscyphus simplex Kirkpatrick 1890: 14 (description), Pl. III, fig. 2 (tube), fig. 2a (cusps) [the species was attributed to G.J. Allman, but no published description or manuscript is available].
Tubularia cornucopia: Broch 1916: 29 [not *Tubularia cornucopia* (Bonnevie, 1898)] [specimens not seen].
Stephanoscyphistoma simplex: Jarms 1990: 11 [mention as a collective group].

History.—As mentioned by Kirkpatrick (1890: 14, footnote), his "bottle" of specimens was labelled with a species name (*Stephanoscyphus simplex*) that he attributed to G.J. Allman. Kirkpatrick noted, however, that he "...had not seen a published description of that species". While studying the cnidarian collection at the NHM we found a small vial (NHM 1878.3.26.11) containing four stephanoscyphistomae. The vial was promptly recognized as taxonomically important because data on the label could be linked to the above account of Kirkpatrick. Based on that evidence, but given our inability to distinguish which of the syntypes was the specimen figured by Kirkpatrick (1890, Pl. III figs 2, 2a) (Fig. 1), we selected one of the better specimens from the series and designated it as the lectotype (ICZN 1999, Article 74).

Material examined.—Syntypes (NHM 1878.3.26.11) collected in the North Atlantic (south of Greenland, 56º11'N, 37º41'W) by H.M.S. *Valorous*, probably in 1875, depth 1450 fathoms (~2650 m).

Description of lectotype.—NHM 1878.3.26.11a (Fig. 2). Solitary polyp (4.18 mm long), with light-brown periderm tube, small basal disc for attachment (0.46 mm diameter) and *Formquotient* 0.138. D/L_{2mm} 0.16, and at the aperture 0,58 (Table 1). Tube surface with a pattern of transverse rings (4-5 rings/0.4 mm) with longitudinal striations, characteristic of Nausithoidae. The tube has only one whorl of internal cusps, arranged as two larger and two smaller perradial cusps. The internal cusps are rectangular.

Description of species.—Solitary polyps (4.18–4.56 mm long, n = 3), with light-brown periderm tube, small basal disc for attachment (0.4–0.46 mm diameter, n = 2) and *Formquotient* at 2 mm height (D/L_{2mm}) 0.16–0.2 (n = 3), and at aperture 0.138–0.150 (n = 3) (see Table 1). Tube surface with pattern of transverse rings (4–5 rings/0.4 mm), with longitudinal striations, characteristic of Nausithoidae (Fig. 3). All tubes observed (n = 3) with a unique whorl of 4 internal cusps (two larger and two smaller perradial ones formed in the same horizontal plane). SEM preparations of the internal whorl of cusps show that the two larger cusps are rectangular in shape and with a smooth surface (Fig. 4). The outline of the internal cusps is higher than broad. All the measurements of the tubes are shown in Table 1.

TABLE 1. Measurements of specimens of *Nausithoe simplex* (Kirkpatrick, 1890), comb. nov. (NHM 1878.3.26.11a, b, d). Symbols: - = no measurement; Dbd = diameter of the basal disc (in mm); Db = diameter just above the basal disc (in mm); Do = diameter of the distal aperture (in mm); Ltot = total length (in mm); D/L_{2mm} = diameter at 2 mm divided by 2; Nwt = total number of whorls of cusps; cusps/whorl = number of cusps per whorl; A-*Formquotient* = actual ratio between the diameter of the distal aperture (Do) and the total length (Ltot); E-*Formquotient* = expected ratio between the diameter of the distal aperture (Do) and length equal to 5 mm.

Specimen	Ltot	Dbd	Db	Do	D/L_{2mm}	A-*Formquotient*	E-*Formquotient*	Nwt	cusps/whorl
NHM 1878.3.26.11a (Lectotype)	4.18	0.46	0.12	0.58	0.16	0.138	0.116	1	4
NHM 1878.3.26.11b	4.4	0.4	0.18	0.7	0.2	0.159	0.140	1	4
NHM 1878.3.26.11d (SEM)	4.56	-	0.1	0.64	0.2	0.140	0.128	1	4

Type locality.—North Atlantic (south of Greenland, 56º11'N, 37º41'W), depth 1450 fathoms (~2650 m).

Comments.—Measurements of specimens NHM 1878.3.26.11a, b and d are presented in Table 1. *Formquotient* is the relation between total length and diameter of the aperture (*cf.* Jarms 1990). The data presented in Table 1 as A-*Formquotient* represent the actual relation. If we assume that the total length (Ltot) was almost equal to 5 mm, then the expected *Formquotient* would be slightly different, *i.e.*, E-*Formquotient* in Table 1 (note that this value is an extrapolation of the actual opening diameter of the tube divided by 5 mm).

References to the species.—Below we present a chronological list of papers that report occurrences of *Stephanoscyphistoma simplex* (as *Stephanoscyphus simplex*). Figure numbers given here refer to those of the cited papers.

– Kirkpatrick (1890: 14) provided a footnote mentioning that 'the specific name *simplex* is on the bottle containing the specimen'. In Plate III there is only a small figure of the polyp attached to the substrate (his Fig. 2) and one with details of the tube with the outer structure, but the drawings of two of the four cusps are only schematic (his Fig. 2a). Recorded from the North Atlantic (56º11'N, 37º41'W).

Unfortunately, accounts in all of the following references do not include mention of the number of internal cusps (except Kramp 1959), and we were not able to locate relevant specimens. Thus, these records of *Nausithoe simplex*, comb. nov., must be considered questionable.

– Leloup (1937: 60–61) considered *S. simplex* to be a synonym of *Nausithoe punctata* Kölliker, 1853 (=*Stephanoscyphus mirabilis*).

– Kramp (1951) described polyps from the north coast of Brazil (02º26'N, 39º26'W) and from two stations between the West Indies and the Bermudas (24º12'N, 63º23'W and 28º25'N, 61º05'W), but Figs 4 and 5 in his work provide no information about structure of the cusps.

– Kramp (1959) provided rather good information about the tube structures of specimens that he attributed wrongly to *Stephanoscyphus simplex* in Figs 1–3. Nevertheless, his Figs 2a and 2b resemble the cusp structures of known species of *Atorella*. That his specimens of *Stephanoscyphus simplex* can be referred to *Atorella* is supported by Fig. 6, plate 1. That illustration shows internal cusps attached to the tube wall with horizontal oval outlines, characteristic of Atorellidae. Parts of his material were ascribed by Morandini & Jarms (2005) to *Nausithoe striata* (Vanhöffen, 1910) and *Atorella sibogae* (Leloup, 1937). The numerous stations where these specimens were collected are shown on the map in Fig. 9.

– Wolff (1961: 139) provided no figure, but reported the occurrence of a single polyp growing over the bivalve *Limopsis* in the East Pacific, collected by the Galathea Expedition (Station 716, at 3570 m).

– Brahm & Mohr (1962) provided no figure. The collection sites are in the Beaufort and Chukchi seas, Arctic Ocean: 71º45'N, 144º55'W (1540 m) and 74º54'N, 165º48'W (471 m).

– Brahm & Geiger (1966) also provided no figure. Their material was collected at 15 stations from 110 to 1440

m in the Arctic Ocean, and from the Peru and Chile trench to the Antarctic Ocean (957–6006 m) (Map, Fig. 1).

– Gili (1986, unpublished thesis) described specimens identified as *Stephanoscyphus simplex* from the Spanish coast (Medas and Cadaqués islands), collected at shallow depths (5–20 m). The author described the presence of 8 cusps per whorl.

– Petersen (1990: 177) and later Schuchert (2001: 42, 2010: 375) stated that the athecate hydrozoan *Tubularia cornucopia* Bonnevie, 1898, after Broch (1916: 29), was actually *Stephanoscyphus simplex*.

– Altuna Prados (1994a: 45–46, unpublished thesis) superficially described as *Stephanoscyphus simplex* material from the Basque coast (Bay of Biscay), at depths between 60–1000 m. The species was not illustrated, and internal cusps of the tubes were not inspected. The records were also cited as *S. simplex* in a species list published by Altuna Prados (1994b: 43, 54). Some of these polyps were later described as a new species, *Nausithoe sorbei*, by Jarms, Tiemann & Altuna Prados (2003).

– Burch & Burch (1995) reported specimens from Hawaii.

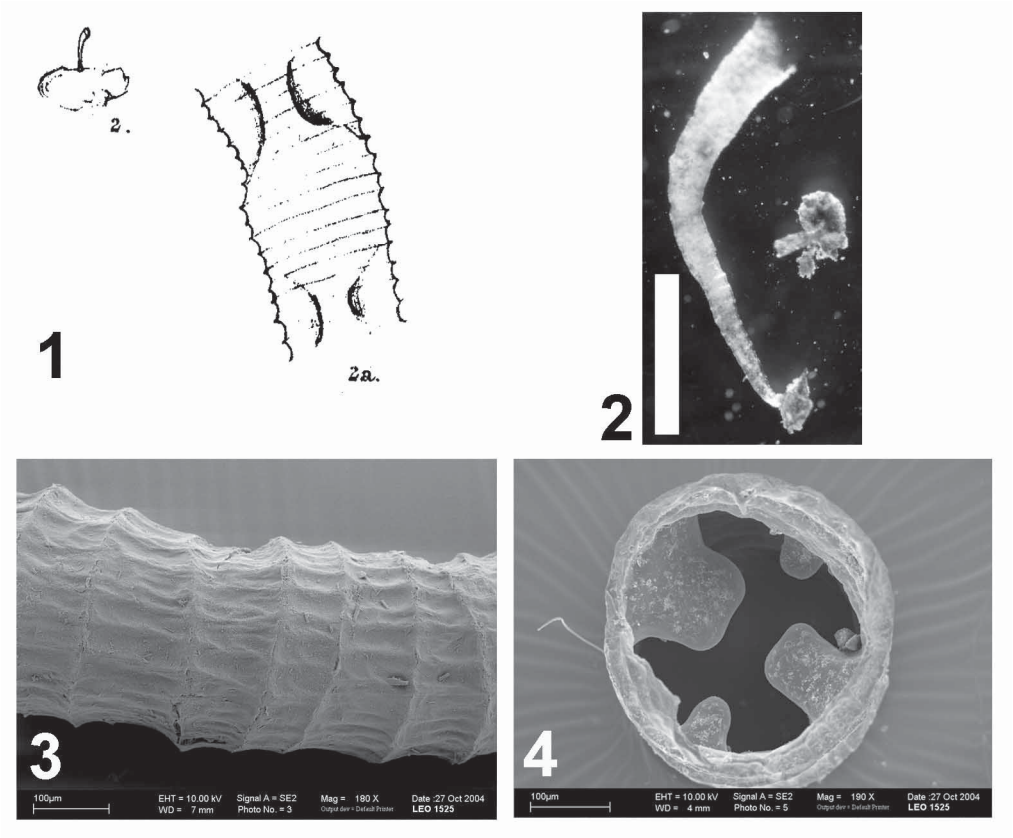

FIGURE 1–4. *Nausithoe simplex* (Kirkpatrick, 1890), comb. nov. **1.** Original figures published in 1890; showing habit of polyp and detail of tube; adapted from the original. **2.** Lectotype (NHM 1878.3.26.11a) on the left and specimen numbered NHM 1878.3.26.11c on the right (note that this specimen is only a basal part of the tube). Scale bar = 2 mm. **3.** Scanning electronic microscopy of tube surface (NHM 1878.3.26.11d). Scale bar = 100 µm. **4.** Scanning electronic microscopy of internal whorl of cusps (NHM 1878.3.26.11d). Scale bar = 100 µm.

Discussion

Four coronate scyphopolyp species (*Stephanoscyphistoma allmani*, *S. bianconis*, *S. corniformis* and *S. simplex*) remain of uncertain taxonomic status because they were described based solely on the periderm tube (Morandini & Jarms 2005). Of these species, *S. allmani* is colonial while the other three are solitary.

Little can currently be said about the status of *Stephanoscyphus bianconis*. It was described by Thiel (1936: 389–390) in an inadequate account of a solitary polyp provided by Lo Bianco (1903: 269). We were unable to locate the type and are uncertain whether it exists. Most accounts in the literature of solitary species of the collective group refer to the other two species, *Stephanoscyphistoma simplex* and *S. corniformis*.

Kramp (1959) distinguished *S. simplex* from *S. corniformis* based mainly on depth distributions, with *S. simplex* being a deep-water form and *S. corniformis* a shallower water species. However, in describing specimens of *S. corniformis*, Kramp (1959: 183) gave hints on what is now referred to as the *Formquotient* (*sensu* Jarms 1990; 1991) (illustrated in his Table 1), indicating that the *S. corniformis* form is generally more slender than that of *S. simplex*. Kramp also used shape of the internal cusps to distinguish the two, with cusps of *S. corniformis* being "…elongated in the longitudinal direction of the tube and have a narrow, slit-shaped base"; and *S. simplex* having cusps with "…broad or fairly broad base and they are broader in transversal than in the longitudinal direction".

Werner (1973) concluded that *Stephanoscyphistoma simplex* and *S. corniformis* were not valid. He suggested that they should be considered species groups or names of convenience because a great number of species resemble these general types.

Following discovery of the type series of *Stephanoscyphistoma simplex*, and examination of their periderm tubes as suggested by Morandini & Jarms (2005), we consider the taxon to be a valid species of *Nausithoe* and remove it herein from the collective group *Stephanoscyphistoma*. The binomen for the species thus becomes *Nausithoe simplex* (Kirkpatrick, 1890), comb. nov. It appears to be a rare species because all coronate polyps collected recently from Greenland and the Arctic Ocean have been identified as *Nausithoe werneri* Jarms, 1990 (Morandini & Jarms 2010).

Kirkpatrick (1890: 14) did not provide a detailed description of *Stephanoscyphistoma simplex*, and his figures could represent any solitary coronate. However, his account of the cruise, and its collection location and year, are sufficient to link the container and original specimens with his remarks about it. While extremely brief, his account of the shape of the tube suggests that the species belongs to *Nausithoe*. Our observation of the type series (from the NHM) and examination of the outer structure of the tubes confirms this supposition. All three of the complete tubes bear but a single whorl of internal cusps (see comment below), a feature observed only in *Linuche unguiculata* (Swartz, 1788), *Nausithoe eumedusoides* (Werner, 1974) and *N. sorbei*. However, *Nausithoe simplex*, comb. nov., has only four cusps in the whorl, a trait observed only in *N. striata* and in a certain region of the tube of *N. thieli* Jarms, 1990 (Jarms 1990; Morandini & Jarms 2005). It is important to note that although the original sketch (here Fig. 1) showed two whorls of cusps, all examined specimens (n=3) had only one whorl. We conclude that the original author may have misinterpreted some debris inside the tube as cusps, or introduced an error in drawing the specimen.

TABLE 2. Measurements comparing different species of the genus *Nausithoe* Kölliker, 1853 having known solitary polyp stages (*N. aurea*, *N. eumedusoides*, *N. globifera*, *N. hagenbecki*, *N. maculata*, *N. marginata*, *N. planulophora*, *Nausithoe simplex*, comb. nov., *N. sorbei*, *N. striata*, *N. thieli*, *N. werneri*). Symbols: D/L_{5mm} = diameter at 5 mm divided by 5; cusps/whorl = number of cusps per whorl; *Formquotient* = ratio between the diameter of the distal aperture (Do) and the total length (Ltot). Data from Morandini & Jarms (2005).

Species	D/L_{5mm}	Formquotient	cusps/whorl	Occurrence
Nausithoe aurea	0.07–0.14	0.07–0.21	16	Brazil
Nausithoe eumedusoides	0.132–0.164	0.13–0.2	1	Mediterranean caves
Nausithoe globifera	0.128	0.134	8	N Atlantic (Morocco)
Nausithoe hagenbecki	0.192	0.08	16	?
Nausithoe maculata	0.112–0.148	0.05–1.01	16	Caribbean
Nausithoe marginata	0.08–0.112	0.063–0.111	8	Mediterranean
Nausithoe planulophora	(mean = 0.132)	0.05–0.12	8, 16	Mediterranean caves
Nausithoe simplex		0.138–0.159	4	North Atlantic (S of Greenland)
Nausithoe sorbei	0.11–0.21	0.009–0.257	1	Bay of Biscay, Azores
Nausithoe striata	0.128	0.114	4	Antarctic Ocean
Nausithoe thieli	0.056–0.072	0.032–0.074	2, 4, 8	Red Sea
Nausithoe werneri	0.096–0.144	0.069–0.113	8	N Atlantic (Morocco), Greenland (Arctic Ocean)

Comparisons of tube measurements and cusps/whorl of the 12 solitary species of the genus *Nausithoe* are presented in Table 2. Although the specimens observed did not reach the minimum length value (5 mm) frequently used for comparison, the values are close. The measurements recorded are close to *N. globifera* Broch, 1914, *N.*

planulophora (Werner, 1971), and *N. striata*, but agree only with *N. striata* in the number of cusps (see Tables 1 and 2, *Formquotient* and cusps/whorl). If we assume that the total length (Ltot) is almost equal to 5 mm, then the expected *Formquotient* would be slightly different. Thus, we hypothesize that the observed *Formquotient* of the specimens would not vary much more (E-*Formquotient*). Based on the previous assumption we can state that, in comparison with other species, the observed values (*Formquotient*) of the specimens are in the range of only *N. aurea* Silveira & Morandini, 1997, *N. sorbei*, and *N. eumedusoides*, and outside the other species. *Nausithoe aurea*, *N. eumedusoides*, and *N. sorbei* have respectively 16, 1, and 1 cusps/whorl. Carefully analyzing Table 2 (*Formquotient*, either actual or expected), the observed polyps of *N. simplex*, comb. nov., resemble those of *N. striata* but differ from that species in having one instead of five whorls of internal cusps.

Although Kramp (1959: 177; 1962: 3) mentioned a strobilating polyp with medusoid stages resembling ephyrae of *Nausithoe*, this was not the chief character that drove our taxonomic determination (see above). Other authors have also hypothesized about medusoid stages released by polyps of *S. simplex* (*e.g.*, Kramp 1951: 126; 1968: 81, probably *Periphylla*), but no clear relation can be established, especially since we maintain that all material studied by Kramp should be re-evaluated. Notably, the life cycle of *Periphylla periphylla* (Péron & Lesueur, 1810), as described by Jarms *et al*. (1999), is holopelagic and does not possess a polypoid stage.

Additional studies of material in Japanese collections are warranted to locate type material of *Stephanoscyphistoma corniformis*. If no available specimens exist, new collections should be made in the type locality or its vicinity to properly re-describe the species and bring stability to the group. Polyps identified as *S. corniformis* were found by Silveira & Morandini (1996) along the southeastern coast of Brazil. Later, different species with solitary polyps was described from the same area (Silveira & Morandini 1997; Jarms *et al.* 2002b). Thus, more than one species may be represented in material identified as *S. corniformis*.

A thorough effort is needed to identify the hundreds of specimens of solitary coronates examined since the 1950s (*e.g.* Kramp 1959; Moore 1961; Burch & Burch 1995), and to examine the abundance of material in museum collections. Identifications should rely on recent advances in systematics of the group based on polypoid stages (see Jarms 1997; Morandini & Jarms 2005, 2010). Such work would advance the taxonomy and systematics of coronates, and result in better knowledge of the distribution of the valid species.

Acknowledgements

We thank Dr. Paul F.S. Cornelius for calling our attention to "small jars" in the collection of the NHM (London, UK). We also thank Mrs. S. Halsey and Mr. A. Cabrinovic (NHM) for valuable support through correspondence, through a museum visit, and in loan of material. We also thank Mrs. R. Walter (Universität Hamburg, Germany) for preparing specimens for SEM. ACM was supported financially by the "Alexander von Humboldt Foundation" and FAPESP (2010/50174-7). We thank referees for careful reading and correction of the manuscript, and also the section editor Dr. Dale R. Calder (ROM, Ontario, Canada). Dr. Alvaro Altuna Prados (INSUB, Okendo Museum, San Sebastián, Spain) helped with some references and corrected the text. Dr. Peter Schuchert (Muséum d'histoire naturelle, Genève, Switzerland) also provided important information.

References

Altuna Prados, A. (1994a) *Estudio faunístico, ecológico y biogeográfico de los cnidarios bentónicos de la costa vasca*. Unpublished PhD thesis, Universidad de Navarra, Pamplona, Spain, 769 pp.

Altuna Prados, A. (1994b) Observaciones biogeograficas sobre los cnidarios bentonicos de la costa Vasca. *KOBIE (Serie Ciencias Naturales*), 22, 41–57.

Bayha, K.M., Dawson, M.N., Collins, A.G., Barbeitos, M.S. & Haddock, S.H.D. (2010) Evolutionary relationships among scyphozoan jellyfish families based on complete taxon sampling and phylogenetic analyses of 18S and 28S ribosomal DNA. *Integrative and Comparative Biology*, 50, 436–455.

Bonnevie, K. (1898) Zur Systematik der Hydroiden. *Zeitschrift für Wissenschaftliche Zoologie*, 63, 465–495.

Brahm, C. & Mohr, J.L. (1962) Report of a scyphozoan *Stephanoscyphus simplex* Kirkpatrick from the Arctic Ocean. *Bulletin of the South California Academy of Sciences*, 61, 64.

Brahm, C. & Geiger, S.R. (1966) Additional records of the scyphozoan *Stephanoscyphus simplex* Kirkpatrick. *Bulletin of the South California Academy of Sciences*, 65, 47–52.

Broch, H. (1914) Scyphomedusae from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. *Reports of the scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition*, 3, 4–20.
Broch, H. (1916) Hydroida (Part 1). *Danish Ingolf Expedition*, 5, 1–66.
Burch, B.L. & Burch, T.A. (1995) New Hawaiian records for *Stephanoscyphus simplex* Kirkpatrick (Cnidaria: Scyphozoa). Records of the Hawaiian Biological Survey for 1994. *Bishop Museum Occasional Papers*, 42, 53.
Calder, D.R. (2009) Cubozoan and scyphozoan jellyfishes of the Carolinian biogeographic province, southeastern USA. *Royal Ontario Museum Contributions in Science*, 3, 1–58.
Chapman, D.M. (1966) Evolution of the scyphistoma. *In:* Rees, W.J. (Ed.), *The Cnidaria and their evolution*, Academic Press, London, pp. 51–75.
Collins, A.G., Schuchert, P., Marques, A.C., Jankowski, T., Medina, M. & Schierwater, B. (2006) Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Systematic Biology*, 55, 97–115.
Galil, B. & Zibrowius, H. (1998) First benthos samples from Eratosthenes seamount, eastern Mediterranean. *Senckenbergiana Maritima*, 28, 111–121.
Gili, J.M. (1986) *Estudio sistemático y faunístico de los cnidarios de la costa catalana*. Unpublished PhD thesis, Universidad Autónoma de Barcelona, Barcelona, Spain, 565 pp.
Goette, A. (1887) Entwickelungsgeschichte der *Aurelia aurita* und *Cotylorhiza tuberculata*. *Abhandlungen zur Entwickelungsgeschichte der Tiere*, 4, 1–79.
Haeckel, E. (1880) *Das System der Medusen. I, 2: System der Acraspeden*. Gustav Fischer, Jena, 361–672 pp.
International Commission on Zoological Nomenclature (1999) *International code of zoological nomenclature*. International Trust for Zoological Nomenclature, London, 306 pp.
Jarms, G. (1990) Neubeschreibung dreier Arten der Gattung *Nausithoe* (Coronata, Scyphozoa) sowie Wiederbeschreibung der Art *Nausithoe marginata* Kölliker, 1853. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 87, 7–39.
Jarms, G. (1991) Taxonomic characters from the polyp tubes of coronate medusae (Scyphozoa, Coronatae). *Hydrobiologia*, 216/217, 463–470.
Jarms, G. (1997) The polyps of Coronatae (Scyphozoa), a review and some new results. *In:* den Hartog, J.C. (Ed.), *Proceeding of the 6th International Conference on Coelenterate Biology, 1995*. Nationaal Natuurhistorisch Museum, Leiden, pp. 271–278.
Jarms, G. (2010) The polyps of Scyphozoa and their impact on jellyfish blooms. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, 45, 17–31.
Jarms, G., Båmstedt, U., Tiemann, H., Martinussen, M.B. & Fosså, J.H. (1999) The holopelagic life cycle of the deep-sea medusa *Periphylla periphylla* (Scyphozoa, Coronatae). *Sarsia*, 84, 55–65.
Jarms, G., Morandini, A.C. & Silveira, F.L. (2002a) Cultivation of polyps and medusae of Coronatae (Cnidaria, Scyphozoa) with a brief review of important characters. *Helgoland Marine Research*, 56, 203–210.
Jarms, G., Morandini, A.C. & Silveira, F.L. (2002b) Polyps of the families Atorellidae and Nausithoidae (Scyphozoa: Coronatae) new to the Brazilian fauna. *Biota Neotropica*, 2, 1–11.
Jarms, G., Tiemann, H. & Prados, A.A. (2003) A new bathybenthic coronate polyp, *Nausithoe sorbei* sp. nov. (Scyphozoa, Coronatae), from the Bay of Biscay and off Azores. *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut*, 100, 1–11.
Kirkpatrick, R. (1890) Report upon the Hydrozoa and Polyzoa collected by P.W. Basset-Smith, Esq., Surgeon R.N., during the Survey of the Tizard and Macclesfield Banks, in the China Sea, by H.M.S. 'Rambler', Commander W.U. Moore. *The Annals and Magazine of Natural History, 6th Series*, 5, 11–24.
Kölliker, A. (1853) *in*: Gegenbaur, C., Kölliker, A. & Müller, H. (1853) Bericht über einige Herbste 1852 in Messina angestellte vergleichend-anatomische Untersuchungen. *Zeitschrift für wissenschaftliche Zoologie*, 4, 299–370.
Komai, T. (1936) On another form of *Stephanoscyphus* found in waters of Japan. *Memoirs of the College of Science, Kyoto Imperial University, Series B*, 11, 175–183.
Kramp, P.L. (1951) Hydrozoa and Scyphozoa. *Reports of the Swedish Deep-sea Expedition. Zoology*, 2, 121–127.
Kramp, P.L. (1959) *Stephanoscyphus* (Scyphozoa). *Galathea Report*, 1, 173–187.
Kramp, P.L. (1962) Reports from the Lund University Chile expedition 1948–49. 44. *Stephanoscyphus corniformis* Komai (Scyphozoa). *Lunds Universitets Årsskrift N.F. Avud. 2*, 58, 3–4.
Kramp, P.L. (1968) The scyphomedusae collected by the Galathea Expedition 1950-52. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 131, 67–98.
Leloup, E. (1937) Hydropolypes et scyphopolypes recueillis par C. Dawydoff sur les côtes de l'Indochine française. II. Scyphopolypes. *Mémoires de Musée Royal d'Histoire Naturelle de Belgique*, 12, 1–73.
Lo Bianco, S. (1903) Le pesche abissali eseguite da F. A. Krupp col Yacht Puritan nelle adiacenze di Capri ed in altre località del Mediterraneo. *Mitteilungen aus der Zoologischen Station zu Neapel*, 16, 109–281.
Marques, A.C. & Collins, A.G. (2004) Cladistic analysis of Medusozoa and cnidarian evolution. *Invertebrate Biology*, 123, 23–42.
Moore, D.R. (1961) The occurrence of *Stephanoscyphus corniformis* Komai (Scyphozoa) in the western Atlantic. *Bulletin of Marine Science of the Gulf and Caribbean*, 11, 319–320.

Morandini, A.C. & Jarms, G. (2005) New combinations for two coronate polyp species (Atorellidae and Nausithoidae, Coronatae, Scyphozoa, Cnidaria). *Contributions to Zoology*, 74, 117–123.
Morandini, A.C. & Jarms, G. (2010) Identification of coronate polyps from the Arctic Ocean: *Nausithoe werneri* Jarms, 1990 (Cnidaria, Scyphozoa, Coronatae), with notes on the biology. *Steenstrupia*, 32, 69–77.
Morandini, A.C. & Jarms, G. (*in preparation*) Checklist of valid names applied to recent jellyfish species (Cnidaria: Scyphozoa and Cubozoa), with comments on the classification.
Péron, F. & Lesueur, C.A. (1810) Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. *Annales du Muséum National d'Histoire Naturelle, Paris*, 14, 325–366.
Petersen, K.W. (1979) Development of coloniality in Hydrozoa. *In:* Larwood, G. & Rosen, B.R. (Eds.), *Biology and systematics of colonial organisms*. Academic Press, London, pp. 105–139.
Petersen, K.W. (1990) Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). *Zoological Journal of the Linnean Society*, 100, 101–231.
Salvini-Plawen, L.v. (1978) On the origin and evolution of the lower Metazoa. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 16, 40–88.
Schuchert, P. (2001) Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). *Meddelelser om Grønland, Bioscience*, 53, 1–184.
Schuchert, P. (2010) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. *Revue Suisse de Zoologie*, 117, 337–555.
Silveira, F.L. & Morandini, A.C. (1996) *Stephanoscyphistoma corniformis* (Komai, 1936) (Cnidaria, Scyphozoa, Coronatae) from the north coast of São Paulo, Brazil. *Semina, Ciências Biológicas / Saúde*, 17, 137–145.
Silveira, F.L. & Morandini, A.C. (1997) *Nausithoe aurea* n. sp. (Scyphozoa, Coronatae, Nausithoidae), a species with two pathways of reproduction after strobilation: sexual and asexual. *Contributions to Zoology*, 66, 235–246.
Swartz, O. (1788) *Medusa unguiculata* och *Actinia pusilla*. *Kungliga Svenska Vetenskaps Akademiens Handlingar*, 9, 198–202.
Thiel, M.E. (1936) Coronatae. *In: Dr. H.G. Bronns. Klassen und Ordnungen des Tierreichs. Zweiter Band: Spongiaria, Coelenterata, Echinodermata, II. Abteilung: Coelenterata, 2 buch Scyphomedusae, 3. Lieferung*. Akademische Verlagsgesellschaft m.b.H., Leipzig, pp. 308–471.
Thiel, H. (1966) The evolution of Scyphozoa: a review. *In:* Rees, W.J. (Ed.), *The Cnidaria and their evolution*. Academic Press, London, pp. 77–117.
Uchida, T. (1969) The interrelationships of scyphozoan class. *Bulletin of the Marine Biological Station of Asamushi*, 13, 247–250.
Vanhöffen, E. (1892) Die Akalephen der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2, 3–28.
Vanhöffen, E. (1910) Die Hydroiden der Deutschen Südpolar-Expedition 1901-1903. *Deutsch Südpolar-Expedition*, 11, 269–340.
Verrill, A.E. (1865) Classifications of polyps (Extract condensed from a synopsis of the Polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S. N.). *Proceedings of the Essex Institute*, 4, 145–152.
Werner, B. (1970) Contribution to the evolution in the genus *Stephanoscyphus* (Scyphozoa Coronatae) and ecology and regeneration qualities of *Stephanoscyphus racemosus* Komai. *Publications of the Seto Marine Biological Laboratory*, 18, 1–20.
Werner, B. (1971) *Stephanoscyphus planulophorus* n. spec., ein neuer Scyphopolyp mit einem neuen Entwicklungsmodus. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 22, 120–140.
Werner, B. (1973) New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria. *Publications of the Seto Marine Biological Laboratory*, 20, 35–61.
Werner, B. (1974) *Stephanoscyphus eumedusoides* n. spec. (Scyphozoa, Coronatae), ein Höhlenpolyp mit einem neuen Entwicklungsmodus. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 26, 434–463.
Wolff, T. (1961) Animal life from a single abyssal trawling. *Galathea Report*, 5, 129–162.